On the Physiological Action of Light.

Abstract of Three Communications read before the Royal Society of Edinburgh.

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THE Authors of this communication have more especially directed their attention to the problem of the specific effect produced on the retina and optic nerve by the action of light. Numerous hypotheses have been made from time to time by physicists and physiologists; but up to the present date our knowledge of the subject is without any experimental foundation. For example, Newton, Melloni, and Seebeck stated that the action of light on the retina consisted of a communication of mere vibrations; Young conjectured that it was a minute intermittent motion of some portion of the optic nerve; Du Bois-Reymond attributed it to an electrical effect; Draper supposed that it depended on a heating effect of the choroid; and Mosier compared it to the action of light on a sensitive photographic plate.

It is evident that, in accordance with the principle of the transference of energy now universally accepted, the action of light on the retina must produce an equivalent result, which may be expressed, for example, as heat, chemical action, or electro-motive power. It is well known that the electro-motive force of a piece of muscle is diminished when it is caused to contract by its normal stimulus, the nervous energy conveyed along the nerve supplying it; and similarly a nerve suffers a diminution of its normal electro-motive force during action. In the same manner, the amount and variations of the electro-motive power of the optic nerve affected secondarily by the action of light on the retina, are physical expressions of

certain changes produced in the latter; or, in other words, are functions of the external exciting energy, which in this case is light. Considerations such as these led us to form the opinion that the problem of what effect, if any, the action of light has on the electro-motive force of the retina and optic nerve, would require for its investigation very careful and refined experiment.

The inquiry divided itself into two parts,—first, to ascertain the electro-motive force of the retina and nerve; and, second, to observe whether this was altered in amount by the action of light. The electro-motive force of any living tissue can be readily determined by the method of Du Bois-Reymond. This great physiologist found that every point of the external surface of the eyeball of a large tench was positive to the artificial transverse section of the optic nerve, but negative to the longitudinal section. This he accomplished by the use of his well-known non-polarizable electrodes, formed of troughs of zinc carefully amalgamated, containing a solution of neutral sulphate of zinc, and having cushions of Swedish filter paper on which to rest the preparation. (To protect the preparation from the irritant action of the sulphate of zinc, a thin film or guard of sculptor's clay, moistened with a ·75 per cent. solution of common salt, and worked out to a point, is placed on each cushion.) These electrodes were connected with a galvanometer, and the preparation was placed so that the eyeball, carefully freed from muscle, rested on the one clay-guard, while the transverse section of the optic nerve was in contact with the other. By following Du Bois-Reymond's method, we have had no difficulty in obtaining a strong deflection from the eyes of various rabbits, a cat, a dog, a pigeon, a tortoise, numerous frogs, and a gold fish. The deflection was frequently so much as to drive the spot of light off the galvanometer scale.

With regard to the second question—namely, Whether, and to what extent, the electro-motive force would be affected by light? we found more difficulty. The method followed was to place the eyeball on the cushions in the manner above de-

scribed, to note the deflection of the galvanometer needle, and then to observe whether or not any effect was produced on the impact of a beam of light, during its continuance, and on its removal. In a few of our earlier experiments we used Du Bois-Reymond's multiplying galvanometer, but finding the amount of deflection obtained was so small that the effect of light could not be readily observed, we have latterly used Sir W. Thomson's exceedingly sensitive reflecting galvanometer, kindly lent us by Professor Tait. We met also with secondary difficulties, such as the dying of the nerve, the impossibility of maintaining an absolutely constant zero, and an absolutely constant amount of polarity, the effects of heat, &c. ; but these difficulties we have overcome as far as possible by the most approved methods. The changes in polarity of the apparatus occurred slowly, and could not be mistaken for the changes produced by the action of light, which we found occurred suddenly, and lasted a short period of time. It is also important to state that the deflections we observed do not at present profess to be absolute, but only relative values. About five hundred observations were made previous to the date of this first communication, and we took every precaution to obtain accurate results. The effects of heat were carefully avoided, by covering over the troughs, on which the eye under examination rested, with a spherical double-shell of glass, having at least an inch of water between the walls.

The results we have arrived at are as follows :—

1. The action of light on the retina is to alter the amount of the electro-motive force to the extent of from 3 to 7 per cent. of the total amount of the natural current.

2. A flash of light, lasting the fraction of a second, produces a marked effect.

3. A lighted match, held at a distance of four or five feet, is sufficient to produce an effect.

4. The light of a small gas flame enclosed in a lantern, and caused to pass through a globular glass jar (12 inches in diameter), filled with a solution of ammoniacal sulphate of

copper or bichromate of potash, has also produced a change in the amount of the electro-motive power.

5. The action of light on the eye of the frog is as follows:— When a diffuse light is allowed to impinge on the eye of the frog, after it has arrived at a tolerably stable condition, the natural electro-motive power is in the first place increased, then diminished; during the continuance of light, it is still slowly diminished to a point where it remains constant; and on the removal of light, there is a sudden increase of the electro-motive power nearly up to its original position. The alterations above referred to are variables, depending on the quality and intensity of the light employed, the position of the eyeball on the cushions, and modifications in the vitality of the tissues.

6. Similar experiments made with the eye of warm-blooded animals, placed on the cushions as rapidly as possible after the death of the animal, and under the same conditions, have never given us an initial positive variation, as we have above detailed in the case of the frog, but always a negative variation. The after inductive effect on the withdrawal of light occurs in the same way.

7. Many experiments have been made as to effect of light from different portions of the spectrum. This was accomplished by causing different portions of the spectrum of the oxy-hydrogen lime-light to impinge on the eye. All these observations tend to shew that the greatest effect is produced by those parts of the spectrum that appear to consciousness to be the most luminous; namely, the yellow and the green.

8. Similarly, experiments made with light of varying intensity, shew that the physical effects we have observed vary in such a manner as to correspond closely with the values that would result if the well-known law of Fechner was approximately true.

9. The method followed in these inquiries is a new method in physiological research, and by the employment of proper appliances, it may be greatly extended, not only with regard to vision, but also to the other senses.

PAPER No. II.—*Read 5th May 1873.*

Since the date of the first communication, we have endeavoured to obtain quantitative results, involving time as a variable element in the case of the action of light on the retina and optic nerve. We have, therefore, found it necessary to construct a true graphical representation of the variations of the electro-motive force occasioned by the impact and cessation of light. It is clear that to register minute galvanometrical alterations, the only plan that could be employed would be to photograph on a sensitive surface, covering a cylinder rapidly revolving on a horizontal axis, the alteration of position of the spot of light reflected from the mirror, just as continuous magnetic observations are registered. As the apparatus required to execute these observations is very complicated, and would require much preliminary practice, we have in the mean time adopted a simpler method of registration. This plan is to note the position of the galvanometer at equal intervals of time, before, during, and after the impact of light on the eye. In these observations we have used a seconds pendulum giving a loud beat. One observer reads aloud the galvanometer; the other marks every interval of two and a-half seconds, registers the numbers obtained, and regulates the supply of light. A little practice in the method above described has enabled us to obtain very satisfactory results, agreeing very closely in different observations, and shewing in a decided way the salient points of the variation curve.

These curves show that on the impact of light there is a sudden increase of the electro-motive force; during the continuance of light it falls to a minimum value, and on the withdrawal of light, there is what we term an *inductive effect*, that

is to say, a sudden increase of the electro-motive force which enables the nerve to acquire its normal energy. The falling off of the electro-motive force by the continued action of light, is the physical representative of what, in physiological language, is called fatigue ; the inductive effect exhibiting the return of the structure to its normal state. Occasionally the impact of light is not followed by a rise in the electro-motive force, but by a diminution. This is probably to be explained by the fact, that the death of the retina and nerve is indicated by a gradual falling of the electro-motive force, and that this change frequently goes on so rapidly that the impact of light is unable to produce any rise. In these circumstances, the spot of light, which before the impact of light was slowly moving downwards, is on the impact steadied for a moment, and then pursues its downward course more rapidly.

We have carried out since last communication, several distinct sets of observations :—

1. We have proved that though there is no difficulty in obtaining a strong current from the skin of the frog, this current is not affected by light. This observation demonstrates that the pigment cells of the skin in the vicinity of the cornea have nothing to do with the results obtained.

2. The current obtained from a mass of the pigment cells of the choroid, does not exhibit any sensitiveness to light.

3. The subcutaneous injection into the frog of woorara, santonin, belladonna, and calabar bean, does not destroy the sensibility of the retina to light.

4. As to the action of the anterior portion of the eye. On carefully bisecting an eye of a frog, so as to remove completely the anterior portion, including cornea, aqueous humour, iris, ciliary-muscle, and lens, and on bringing the retina into actual contact with one of the clay pads, we readily obtained a large deflection, which was as sensitive to light as when the whole eye was employed, thus eliminating any possibility of the contraction of the iris under the stimulus of light having to do with the results previously obtained.

5. On using the anterior portion of the eye, so that the cornea and posterior surface of the crystalline lens were the poles, we obtained a large deflection, which was, however, insensible to light.

6. The sclerotic and nerve without the retina, in the same manner, gave a large natural electro-motive force, also not sensitive.

7. The distribution of the electro-motive force between the different portions of the eye and cross section of the nerve may be stated as follows: The most positive structure is the cornea, then the sclerotic, then the longitudinal surface of the nerve; the cornea is also positive to the posterior surface of the crystalline lens, and the retina itself seems to be positive to the transverse section of the nerve.

8. As to the effects produced by lights of different intensities. If a candle is placed at a distance of one foot from the eye, and then is removed ten feet, the amount of light received by the eye is exactly one hundredth part of what is got at a distance of one foot, whereas the electro-motive force, instead of being altered in the same proportion, is only reduced to one-third. Repeated experiments made with the eye in different positions has conclusively shewn that a quantity of light one hundred times in excess of another quantity, only modifies the electro-motive force to the extent of increasing it three times as much, certainly not more.

9. It was apparent to us that these experiments would ultimately bear upon the theory of sense-perception as connected with vision. It is now generally admitted that no image, as such, of an external object, is conveyed to the sensorium, but that in reality the brain receives certain impressions of alterations taking place in the receiving organ. The natural query then arises,—are the physical effects we have described and measured really comparable in any way with our sensational differences in light perception, when we eliminate all mental processes of association, &c., and leave only perception of difference of intensity? In other words, are these changes the

representative of what is conveyed to the sensorium? It would appear, at first sight, that this problem is altogether beyond experimental inquiry. There is, however, a way of arriving at very accurate measures of the variation of our sensational differences in the case of light, and this has been developed theoretically and experimentally by the justly renowned physiologist Fechner. Stating the law of Fechner[1] generally, we may say, the difference of our sensations is proportional to the logarithm of the quotient of the respective luminous intensities. A recent series of experiments by Dalbœuf[2] has entirely confirmed the truth of this law. If, therefore, the observed differences in electro-motive power, registered under conditions of varying luminous intensity, agree with this law of Fechner, regulating our sensational impressions, then there can be little doubt these variations are the cause of, and are comparable to, our perception of sensational differences. Now, we have stated above, that with a quantity of light 100 times in excess of another quantity, the electro-motive force only becomes three times greater. According to Fechner's law, we may say the difference of our sensations, with that variation in the amount of luminous intensity, would be represented by 2, the logarithm of 100. Our experimental results being as 3 to 1, the difference is also 2, thus agreeing very closely. It is to be remembered, however, that these results have been obtained by experiment on the eye of the frog, but similar changes have been observed in the eyes of mammals. In the latter, however, the amount of alteration is not so great, in all probability owing to the rapid death of the parts.

10. When one clay-point is placed in contact with the cornea or nerve, and the other with the section of the optic lobe, a current is at once obtained which is sensitive to light. In this experiment the eye is left in the orbit, and the nerve is uninjured. Thus, the effect of light on the retina has been traced into the brain.

[1] Fechner, *Elemente des Psychophysik.* Helmholtz, *Optique physiologique.*

[2] Recent Memoir to Belgian Academy.

PAPER No. III.—*Read 2d June 1873.*

Since the date of our last communication, we have continued our investigations, with the following results :—

1. The light from a beam of uncondensed moonlight, though of weak intensity, and almost entirely free from heat rays, is still sufficient to alter the electro-motive power of the nerve and retina.

2. We have examined the phenomenon in the eyes of the following animals :—

(1.) The common newt—*Triton aquaticus ;* (2.) The goldfish—*Cyprinus auratus ;* (3.) The rockling—*Motella vulgaris ;* (4.) The stickleback—*Gasterosteus trachurus ;* (5.) The common edible crab—*Cancer pagurus ;* (6.) The swimming crab—*Portunus puber ;* (7.) The spider crab—*Hyas coarctatus ;* (8.) The hermit crab—*Pagurus Bernhardus ;* and (9.) The lobster—*Homarus vulgaris.*

The general results with the eyes of these various animals, were similar to those we have previously described. The eye of the goldfish and rockling, both sluggish fishes, were found to resemble each other, inasmuch as the variations in the electro-motive force were slow, and in this respect they presented a marked contrast to those of the active and alert stickleback, the eye of which was very sensitive to light.

The experiments on the eyes of crustacea are of importance, because they show that the action of light on the compound eye is the same as on the simple eye, namely, that it alters the amount of the electro-motive force of the sensitive surface. The eye of the lobster was found to give a deflection of about 600 galvanometrical degrees, the scale being placed at a dis-

tance of about twenty-six inches. Light produced a variation in this deflection of about 60 degrees,—that is, about ten per cent., the largest amount of variation we have yet observed in any eye. It was also demonstrated that the effect of light, diminished in intensity by distance, was exactly what was observed in the case of the simple eye. For example, at the distance of one foot, a variation to the extent of about 100 degrees was observed. At a distance of ten feet, with 1-100th part of the amount of light, the effect was not 1 degree, but 20 degrees, or one-fifth of the total amount observed at one foot.

2. The action of light on the electro-motive force of the living eye in cats and birds (pigeon and owl) has been observed. In our earlier experiments, we found great difficulty in observing sensitiveness to light in the eyes of mammals and birds, when these were removed with the utmost despatch from the orbit of the animal immediately after death. This was evidently owing to the fact, that the sensibility of the nervous system in these animals disappears quickly after the withdrawal of healthy blood. It, therefore, became necessary to perform the experiment on the living animal. This was done by first putting the cat or bird under the influence of chloroform, then fixing it by a proper apparatus so that the head was perfectly immoveable, and lastly removing the outer wall of the orbit with as little disturbance to the ciliary vessels as possible. The optic nerve was now cut, the transverse section directed upwards, and the clay points of the electrodes were now adjusted, one to the transverse section of the nerve, and the other to the cornea. With these arrangements, we at once found a strong current extremely sensitive to light.

4. The effect was traced into the optic lobes of a living pigeon under chloroform. The following were the results of this observation :—*a.* When one pole was applied to the left optic lobe, and the other to the cornea of the right eye, a deflection was obtained which was sensitive to light; *b.* When the pole was removed from the right eye and applied to the cornea of the left, a smaller deflection was obtained, also

sensitive to light; and *c*. When light was allowed to impinge on both eyes, while the one pole was in contact with either eye and the other with the left optic lobe, the result was nearly double that produced by the impact of light on one eye alone, either right or left. These effects may be explained by the decussation of the optic nerves in the optic commissure.

5. The eye of a snake[1] was examined, and in its action resembled that of the frog.

6. We are therefore now in a position to state, that the law of the variation in the electro-motive force of the retina and optic nerve, holds good in the following groups of the animal kingdom, Mammalia, Aves, Reptilia, Amphibia, Pisces, and Crustacea.

7. Many experiments have been made which prove that the psychophysical law of Fechner, alluded to in previous communications, is not dependent only on perception in the brain but in part on the structure of the eye itself. The effects which occur on, during, and after the action of light on the retina, also take place after the eye has been removed from all connection with the brain. Thus the law of Fechner, is not, as has been hitherto supposed, a function of the brain alone, but is really a function of the terminal organ, the retina.

8. We have also employed a new method of registering galvanometrical variations, which may be of service in many physical and physiological researches. This consists in placing at the proper distance from the galvanometer, instead of the ordinary graduated scale, the surface of a cylinder covered with paper, and moving on a horizontal axis by clock-work. The spot of light reflected from the galvanometer mirror is rendered more precise by having the shade of the galvanometer lamp blackened over the entire surface, with the exception of a spot about three millimetres in breadth, in the centre of which a line or cross is made of soot. The image of this line

[1] Kindly sent us by Mr Bartlett, of the Zoological Gardens, Regent's Park. We have also to acknowledge the kindness of Mr Lloyd, Manager of the Crystal Palace Aquarium, who supplied us with three specimens of *Eledone* (a cuttle-fish, to represent *Mollusca*), but none arrived alive.

or cross is of course reflected by the mirror upon the cylinder. When the cylinder is set in motion by the clock-work, the spot of light may be accurately followed by the hand of the observer, after a little practice, with a fine brush moistened with ink. The cylinder we employed performed a complete revolution in eighty seconds. This time was divided into four equal parts each representing twenty seconds, by four lines drawn transversely at equal intervals across the paper on the cylinder. The first space, between lines one and two, represented twenty seconds, in which the eye was in the dark, and in which the electro-motive force is represented by a straight line; the second space, between lines two and three, represented twenty seconds, during which the effect of the impact of light took place, and in which the variation of the electro-motive force is indicated, either by a curve to the right or to the left; the third space, between lines three and four, represented twenty seconds of continued action of light, during which the electro-motive force gradually rises; and lastly, the fourth space, between lines four and one (the point of starting), represented twenty seconds, during which the electro-motive forces at first rises on the withdrawal of light, and afterwards sinks rapidly.